

FORAGING AND RECRUITMENT IN
PONERINE ANTS: SOLITARY HUNTING IN
THE QUEENLESS *OPHTHALMOPONE BERTHOUDI*
(HYMENOPTERA: FORMICIDAE)

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INTRODUCTION

Recent studies have indicated that, in ponerine ants, a eusocial organization is viable without the presence of a queen caste. In *Rhytidoponera* (Haskins and Whelden, 1965; Ward, 1983; Pamilo *et al.*, 1985) and *Ophthalmopone berthoudi* (Peeters and Crewe, 1985), some of the workers (= gamergates; Peeters and Crewe, 1984) engage in sexual reproduction. Although there is still reproductive division of labor within the colonies, the loss of the queen caste represents a retrogression since the replacement egg-layers lack specialized ovaries. It is of interest to discover whether other aspects of the colonial organization of permanently queenless ponerines have changed with this modification in the reproductive structure. One consequence of this change is that queenless colonies have low levels of relatedness among nest inhabitants (there are many mated laying workers), and Ward (1981, 1983) has suggested that this leads to lower levels of altruistic behavior. Thus Ward would expect colony defence and foraging efficiency to be less well-developed in these species. The natural history of more species of queenless ponerines needs to be documented in order to test the validity of this opinion.

The genus *Ophthalmopone* belongs to the tribe Ponerini (subtribe Poneriti), and is derived from *Pachycondyla* (W. L. Brown, pers. comm.). *O. berthoudi* Forel occurs in Angola, Zambia, Zimbabwe, Mozambique, and the eastern part of South Africa (Prinz, 1978). The workers are monomorphic, and it is exclusively termitophagous. Alfred Ilg described columns of hunting ants in *O. ilgi*

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(reported in Forel, 1928), and it has been assumed that group-raiding behavior occurs in the whole genus (Wheeler, 1936; Wilson, 1958). The colonies of *O. berthoudi* are polydomous (Peeters, 1984).

NATURAL HABITAT AND METHODS

This study was carried out in one locality in Mkuzi Game Reserve (north-eastern Natal, South Africa), during 1981–1983. Over 100 working days were spent in the field. Mkuzi is semi-arid (Goodman, 1981), with a hot humid summer from mid-September to the end of March. The rainfall is highly seasonal, peaking in February and lowest in June. The greatest variability in the mean monthly rainfall occurs during the dry winter months. The colonies of *Ophthalmopone berthoudi* occurred in open woodland with a grass component less than 1%. The micro-distribution of these ground-dwelling ants is influenced by soil characteristics. They nest in sandy clay loam which is free-draining (i.e. no sub-surface clay pans). The surface is slightly capped and compacted; this increases the run-off and decreases the infiltration. The ponerine community at this location also included *Plectroctena mandibularis* and *P. conjugata*, *Pachycondyla* sp. (*soror*-complex) and *P. krugeri*.

Various nests were selected for intensive study, and every ant coming in or out of these was colour marked. Some ants were also collected inside the nests and marked. Spots of paint were applied to 1–5 pre-selected dorsal positions and, with a choice of five colours (Humbrol enamel paint), a sufficient number of unique combinations was generated. The ants did not lose their marks with time because painted ants were observed for several months and unexpected color codes were never recorded (the paint holds well to the pubescent cuticle). The activities of individual ants were monitored for varying numbers of days, with the help of a portable tape recorder. Many of the nests were excavated at the end of field visits.

FIELD OBSERVATIONS

Nest description

Nests consisted of a number of underground chambers and galleries with no distinct spatial arrangement, and seldom extended deeper than 50 cm. Nest entrances were simple holes in the ground with little or no accumulation of soil around the hole. Active termite

tunnels were sometimes intimately associated with the ant nests, and we suggest that the ants modify abandoned termite tunnels and use them as nests.

Since adults and brood were frequently carried between nests, we soon determined that a single colony occupies more than one nest site (= polydomy). Colony units were made up of 2–7 nests, and these nests were separated by distances varying from 30 cm to 75 m. None of the nests were connected underground, even those with entrances very close to each other.

Individual nests contained variable numbers of adults (mean = 186 ± 151 s.d., range = 20 – 840, $n = 34$) and brood. Four colonies had all their component nests excavated, and the following estimates of total population were obtained (mean = 517):

January 1981: 3 nests, 453 adults (84, 142, 227).

April 1981: 3 nests, 838 adults (445, 75, 318).

December 1981: 2 nests, 311 adults (261, 50).

February 1982: 5 nests, 464 adults (168, 124, 72, 80, 20).

Patterns of activity

The ants were observed outside their nests throughout the year, although the level of above ground activity decreased during the dry winter months. A subjective impression was that foragers then spent more time away on single hunting expeditions, and that they returned with fewer termites. This is probably linked to decreased termite availability; the dry soils and the low temperatures at night lead to a reduction in the nocturnal activity of the termites.

Diurnal patterns of activity varied during the year. The ants remained outside the nests throughout the day during winter, but during the rest of the year, above ground activities stopped during the middle of the day. The biphasic summer pattern (04h30–10h00; 17h00–sunset) appeared to be regulated by soil temperatures. Indeed, foragers returning to their nests towards the end of the morning period of activity repeatedly climbed up short grass stems. They remained there for short periods before they ventured on the ground again and ran across to the next plant. When the ground surface became very hot (50°C), the ants stayed inside their nests. On cool, cloudy or rainy summer days, foraging continued for longer periods and even for the whole day.

Activities around the nest entrances

Excavation occurred frequently after rain, with soil being brought out of the nests to the surface. Nest sanitation was a distinct activity, whereby workers came up to the surface and discarded pellets of termite remains, as well as empty cocoons. The former consisted of jaws, limbs, and other bits of exocuticle, which were all packed into a distinctive rough-looking ball. These pellets were carried for 1–5 m before being left on the ground; they were never discarded close to the nest entrances. Individual cleaners repeatedly dropped their pellets in the same place.

No natural instances of predation on *O. berthoudi* were recorded, but it is suspected that lizards feed on the ants. A number of arthropods (beetles, spiders, ant lion larvae) were observed trying to steal the termites retrieved by foragers.

Carrying behavior: adult and brood transfer

Adult carrying occurred daily and was preceded by a stereotyped "invitation behavior". This involved vigorous antennation and was similar to that described by Möglich and Hölldobler (1974) for *Rhytidoponera metallica*. However, the carrying posture in *O. berthoudi* is completely different (Fig. 1), with the recruit carried on its side underneath the other ant. Not all invitation interactions were followed by carrying, and the outcome seemed influenced by the age and motivation of the participants.

Adults were carried between existing nests of the same colony. Single cocoons, single larvae of all sizes and packets of 3–14 eggs were also frequently transported above ground. Males were carried between nests during January–February. Different recruiters that were active between the same pairs of nests seldom followed the same route, and the paths were sometimes strikingly different. This is further evidence that the nests are not connected together by chemical trails.

Nest emigration is a frequent occurrence in ponerine ants. Species which do not lay chemical trails for social coordination use social carrying or tandem running (e.g. Möglich and Hölldobler, 1974; Fukumoto and Abe, 1983; Hölldobler, 1984; Traniello and Hölldobler, 1984; Fresneau, 1985). Both these primitive recruitment techniques are preceded by the same invitation behavior, and in *Pachycondyla obscuricornis* they are used alternatively to recruit

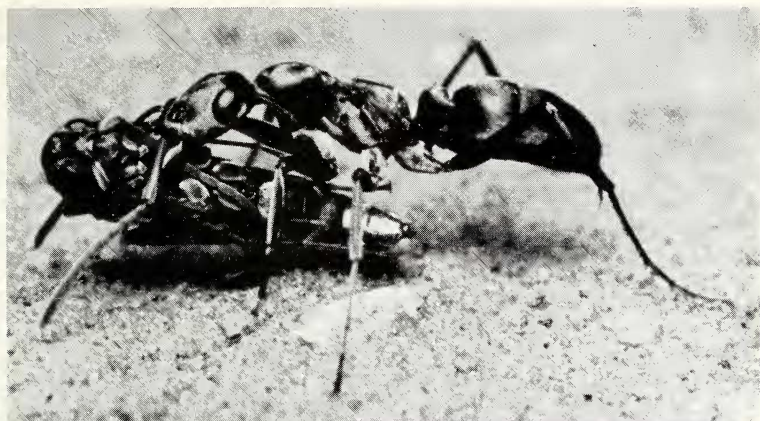


Figure 1. Worker of *Ophthalmopone berthoudi* carrying a male between two nests—workers are carried in an identical way.

sexuals or workers (Traniello and Hölldobler, 1984). In *O. berthoudi*, social carrying is not only used during the evacuation of old nests and the settlement of new ones, but is a habitual, routine event between established nests. An ant carried to another nest in a colony remains associated with it; if it was active above ground, it will return to this new nest after future performance of its task. While being carried, an ant is also provided with visual navigation cues which enable her to return to the nest of origin. When marked recruiters and recruits came apart outside the nests, the latter were unable to proceed but could walk back to the nest from which they originated. A detailed analysis of the pattern of recruitment between nests will be presented elsewhere. While the proximate adaptive significance of inter-nest transfers is unclear, they have the effect of maintaining contact between the nests of polydomous colonies.

Foraging behavior

O. berthoudi feeds exclusively on termites. The ants only hunted those species which foraged in accessible places, and termite nests were never raided. Cooperative hunting was never observed. Three termite species seemed to make up most of the ants' diet. *Macrotermes natalensis* and *Odontotermes badius* forage principally on

wood-, grass-, or leaf-litter on the surface, covering these with a thin layer of soil and feeding beneath this protective cover. Chemical cues contained in fresh soil sheeting of these two termite genera are detected by scout ants of *Megaponera foetens* (Longhurst and Howse, 1978); this effect was not investigated in the present study. Foragers of *O. berthoudi* broke open the soil sheeting or looked for natural openings. Termites were captured one by one; the prey was held in the ants' mandibles, impaled on the sting and flung underneath the body to the rear. After catching up to 15 termites in this way, the foragers gathered most of the semi-immobilized bodies and stung them once again. They packed the termites between their mandibles and brought them back to the nest. *O. berthoudi* also preyed on *Hodotermes mossambicus*, which are grass-harvesters on the surface, and which sporadically exit in small groups from underground galleries. The ants located these visually, and captured single termite workers which were immobilized with the sting. Successful foragers only remained inside their nest for a short while before they reappeared (in laboratory nests they leave their prey in the entrance chambers), and revisited the same locations. Foragers were often found with missing limbs, and such injuries are presumably sustained during hunting.

Recruitment never occurred, and single foragers independently exploited a food source until it was exhausted. Social facilitation was observed in laboratory nests however; the return of successful foragers induced others to go out and hunt, but to no particular location. The lack of cooperation between hunters is associated with the absence of trails in this species. The distinctive trail-laying gait was never observed, and simple experiments showed that foragers do not become disoriented when soil ahead of them is disturbed. Instances of tandem running were never seen. Some kind of discrete marking was sometimes observed however. Workers stood momentarily still and rubbed the ventral tip of their gaster sideways over objects lying on the ground (e.g. pebbles, dead leaves, sticks, . . .); marking was never done directly onto the bare ground. This behavior was especially conspicuous around nest entrances after rain, and also occurred when some foragers walked away from their nests. We suggest that ants which are unfamiliar with a new area outside their nests lay these marks and then use them as personal orientation cues

on their return. Similarly, scouts in *Pachycondyla tesserinoda* deposit and use scattered chemical orientation marks which have no recruiting effects (Jessen and Maschwitz, 1985).

Foraging originated from every nest and marked hunters were always recorded as returning to their nest of origin in a colony. Some foragers did not hunt around their own nests, and travelled long distances to hunt in areas nearer other nests in the colony, where they had been observed to be previously active. On consecutive days, the same individuals returned to the same part of their colony's home range.

DISCUSSION

Ophthalmopone berthoudi invariably hunts alone; this is in conflict with previous references to this genus in the literature. There is no cooperation among foragers, either through the transfer of information about the location of new sources of prey, or through direct assistance during the killing and retrieving of prey. Many other species of ponerines are also solitary predators (Table 1), although they are in many cases more opportunistic in their choice of prey. Group retrieving (involving a small number of workers) is occasionally seen in some species of solitary hunters (when prey is too large or numerous to carry), but this cooperation is not always a consequence of recruitment, i.e. a huntress can attract nestmates in her immediate vicinity through the release of alarm pheromones (*Amblyopone pallipes*; Traniello, 1982), which is not equivalent to returning to her nest to recruit one or more nestmates to the prey (e.g. *Rhytidoponera purpurea*; Ward, 1981). In *Plectroctena conjugata* (Peeters, unpublished), several foragers are sometimes led together to a hunting area, but they capture prey and return to the nest independently.

Solitary predation contrasts with the elaborate systems of recruitment and cooperative hunting displayed by other ponerine species. Fletcher (1973) has critically reviewed column-raiding in the Ponerinae. The comparative overview in Table 1 reveals that simple and complex hunting strategies occur in different species irrespective of phylogenetic relationships. Thus *O. berthoudi* and *Megaponera foetens* are closely related (W. L. Brown, pers. comm.) but

Table 1. Overview of the foraging techniques exhibited in the Ponerinae (only a few species of *Leptogenys* have been included). The process of hunting living prey (=predation) is broken up into raiding (getting to the prey) and retrieving, a distinction made by Wilson (1958). "Group" refers to a small number of participants (less than 10-15), while "column" involves many ants walking together in one of several distinct files. The species mentioned are all predatory, and they belong to the following tribes and sub-tribes (Brown, 1958, 1960, 1975, pers. comm.): (1) Amblyoponini; (2) Cerapachyini; (3) Ectatommini; (4) Platythyreini; (5) Ponerini, a: Odontomachiti, b: Poneriti, c: Leptogenyiti.

Recruitment technique associated with foraging	Species recorded in the literature (and tribe)	Hunting strategy	References
no chemical trails, no recruitment	<i>Amblyopone pluto</i>	(1) solitary	Gotwald & Lévieux 1972
	<i>A. pallipes</i>	(1) solitary	Traniello 1982
	<i>Rhytidoponera</i> sp. 12	(3) solitary*	Pamilo et al. 1985
	<i>Ectatomma ruidum</i>	(3) solitary	Lachaud 1985
	<i>Platythyrea conradti</i>	(4) solitary	Lévieux 1976
	<i>Odontomachus bauri</i>	(5a) solitary	Jaffe & Marcuse 1983
	<i>Ophthalamopone berthoudi</i>	(5b) solitary	this study
	<i>Diacamma rugosum</i>	(5b) solitary	Fukumoto & Abe 1983
	<i>Dinoponera gigantea</i>	(5b) solitary	Haskins & Zahl 1971
	<i>Pachycondyla obscuricornis</i>	(5b) solitary	Traniello & Hölldobler 1984
	<i>P. (=Neoponera) apicalis</i>	(5b) solitary*	Fresneau 1985
	<i>Pachycondyla tesserinoda</i>	(5b) solitary, group retrieving large prey	Maschwitz et al. 1974
	<i>Mesoponera caffraria</i>	(5b) solitary, group raiding and retrieving	Agbogba 1984
	<i>Hypoconera</i> sp.	(5b) solitary, group retrieving (large prey)	Agbogba 1984
recruitment by tandem-running			

rudimentary chemical recruitment (short-lived trails)	<i>Rhytidoponera chalybaea</i>	(3)	solitary, group retrieving*	Ward 1981
	<i>R. purpurea</i>	(3)	same, with long-range trails to aphids	Ward 1981
	<i>Plectroctena mandibularis</i>	(5b)	solitary, group retrieving (large prey)	Fletcher 1973
advanced chemical recruitment (more persistent trails, larger groups)	<i>Paltothyreus tarsatus</i>	(5b)	solitary, group raiding and retrieving*	Hölldobler 1984
	<i>Leptogenys attenuata</i>	(5c)	solitary, also group raiding (2-5 ants)	Fletcher 1971
	<i>Cerapachys turneri</i>	(2)	column raiding (on ant nests)	Hölldobler 1982
	<i>Paraponera clavata</i>	(3)	solitary†, group foraging to nectar	Breed & Bennett 1985
	<i>Pachycondyla laevigata</i>	(5b)	column raiding, solitary retrieving?	Hölldobler & Traniello 1980
	<i>P. commuata</i>	(5b)	column raiding and retrieving	Mill 1984
	<i>Megaponera foetens</i>	(5b)	column raiding (complex)	Longhurst & Howse 1979
	<i>Simopelta oculata</i>	(5b)	column raiding (on ants)	Gotwald & Brown 1966
	<i>Leptogenys chinensis</i>	(5c)	group raiding (2-6), solitary retrieving	Maschwitz & Schönegge 1983
	<i>L. nitida</i>	(5c)	group raiding (few ants) and retrieving	Fletcher 1971
	<i>L. kitteli</i>	(5c)	column raiding (40-60) and retrieving	Baroni Urbani 1973
	<i>Onychomyrmex</i>	(1)	swarm raiding (destination of column is not predetermined)	Brown 1960, Hölldobler et al. 1982

* also scavengers

† along established trunk trails

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	<i>Rhytidoponera</i> sp. 12	(3)	solitary*	Pamilo et al. 1985
	<i>Ectatomma ruidum</i>	(3)	solitary	Lachaud 1985
	<i>Platythyrea conradi</i>	(4)	solitary	Léveux 1976
	<i>Odontomachus bauri</i>	(5a)	solitary	Jaffe & Marcuse 1983
	<i>Ophidomachus berthoudi</i>	(5b)	solitary	this study
	<i>Diacamma rugosum</i>	(5b)	solitary	Fukumoto & Abe 1983
	<i>Dinoponera gigantea</i>	(5b)	solitary	Haskins & Zahl 1971
	<i>Pachycondyla obscuricornis</i>	(5b)	solitary	Traniello & Hölldobler 1984
	<i>P. (=Neoponera) apicalis</i>	(5b)	solitary*	Fresneau 1985
	<i>Pachycondyla tessierimoda</i>	(5b)	solitary, group retrieving large prey	Maschwitz et al. 1974
recruitment by tandem-running	<i>Mesoponera caffraria</i>	(5b)	solitary, group raiding and retrieving	Agbogba 1984
	<i>Hypoponera</i> sp.	(5b)	solitary, group retrieving (large prey)	Agbogba 1984
rudimentary chemical recruitment (short-lived trails)	<i>Rhytidoponera chalybea</i>	(3)	solitary, group retrieving*	Ward 1981
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	<i>Pachycondyla laevigata</i>	(5b)	column raiding, solitary retrieving?	Hölldobler & Traniello 1980
	<i>P. commutata</i>	(5b)	column raiding and retrieving	Mill 1984
	<i>Megaponera foetens</i>	(5b)	column raiding (complex)	Longhurst & Howse 1979
	<i>Simopelta oculata</i>	(5b)	column raiding (on ants)	Gotwald & Brown 1966
	<i>Leptogenys chinensis</i>	(5c)	group raiding (2-6), solitary retrieving	Maschwitz & Schönegge 1983
	<i>L. nuda</i>	(5c)	group raiding (few ants) and retrieving	Fletcher 1971
	<i>L. kitteli</i>	(5c)	column raiding (40-60) and retrieving	Baroni Urbani 1973
	<i>Onychomymex</i>	(1)	swarm raiding (destination of column is not predetermined)	Brown 1960, Hölldobler et al. 1982

* also scavengers

† along established trunk trails

exhibit solitary hunting and column raiding respectively, and members of the genus *Pachycondyla* exhibit a range of hunting strategies. Furthermore, representatives of each of four tribes hunt in well-coordinated raids (Table 1). These data emphasize that foraging characteristics are the product of the unique selective pressures facing each species. The evolution of these characteristics is not governed by anatomical constraints, e.g. all members of the sub-tribe Poneriti seem to have the exocrine glands necessary for recruitment, but only some of them hunt in groups. In addition, some solitary-hunting species have recruitment capabilities which they do not use during foraging, e.g. *Diacamma rugosum*, *Dinoponera gigantea* and *Pachycondyla* (= *Neoponera*) *apicalis* use tandem-running during nest emigration only (Fukumoto and Abe, 1983; Overal, 1980; Fresneau, 1985).

Wilson (1958) suggested that group hunting only becomes selectively advantageous with respect to certain prey preferences. This is evident for species which prey on large arthropods or on the brood of other ants. However, strictly termitophagous species include both solitary and column hunters, i.e. a number of strategies are appropriate to exploit this strongly-clumped prey. Column raiding appears to have evolved a number of times and from different behavioral antecedents (Furthermore, different exocrine glands are involved in recruitment.), and this term thus describes a range of "variations on one theme". Indeed in some species, group raiding is followed by solitary retrieving of the prey. The occurrence of group hunting is unlikely to be related to one ecological factor only.

There has not been a phylogenetic trend towards the elaboration of patterns of cooperation and recruitment during predation in the Ponerinae, and these characteristics can vary from species to species regardless of the nature of the reproductive system. Indeed, group foraging is characteristic of the genus *Leptogenys*, and this behaviour is unaffected by the change to gamergate breeding which has occurred in *L. schwabi* (M. Zini, in prep.). Thus we reject the possibility that the simple hunting strategy seen in *O. berthoudi* is a secondary modification caused by a reduction in altruism in colonies with numerous matriline. We note that solitary-hunting species with a highly-specific diet are more vulnerable to seasonal fluctuations in prey availability. Rather than implying that elimination of the queen caste would result in a simplification of social

relationships, attempts should be made to understand how it might have arisen as an *effect* of various attributes of the life histories.

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